

Effects of Current Velocity on the Physical Structuring of Diatom (Bacillariophyceae) Communities¹

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ABSTRACT. Diatom-dominated periphyton communities growing under different current velocities on pre-cleaned rock substrates were harvested from the Maumee River, Ohio, during the winter of 1980. Analysis of the initial stages of colonization using scanning electron microscopy revealed that the communities were compositionally very similar, but that diatom cell densities were more than three times as dense in the slow current (15 cm/s) as in the fast current (40 cm/s). The diatom communities were described quantitatively in an attempt to determine how physical structuring was influenced by current velocity. Slow-current communities were shown to exhibit more vertical height development. Slow-current communities were also shown to create and develop more usable substrates for colonization within the community. Both of these aspects of physical structuring led to greater community diversity and more rapid successional development for communities in the slow current.

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INTRODUCTION

The effects of current on the periphyton of lotic environments have received critical attention in recent years. It has been shown that a change in current can change the composition and abundance of attached algal communities in laboratory streams (McIntire 1966, 1968a, Zimmerman 1961a, b, 1962, cited in Hynes 1970). Others have found similar results in field observations (Jones 1951, Guntow 1955, Whitford 1956, Blum 1960, Reisen and Spencer 1970, Keithan and Lowe 1985).

Current also affects various measures of organic production. An increase in current has been shown to increase primary production (Pfeifer and McDiffitt 1975, Rodgers and Harvey 1976, Rodgers et al. 1978, Keithan and Lowe 1985), respiration, and mineral uptake (Whitford and Schumacher 1961, 1964, Schumacher and Whitford 1965). McIntire (1966, 1968a,b) showed that, as current velocity increases, the percent organic matter

is greater and the accumulation and export of biomass increase.

In a preliminary report of this investigation, Lamb and Lowe (1981) discussed the effects of current velocity on the initial stages of periphyton development. Two diatom-dominated communities (one developed in a fast current and one developed in a slow current) were compared and found to be structurally different. Cells in the slow-current community tended to grow upright (perpendicular to the substrate), cell densities were higher, and single cells often gave rise to rosettes and sprays. Cells of the same species tended to grow prostrate in the fast-current community.

We hypothesized that a relationship exists between cell densities and the physical structuring of communities. Slow current velocity allows cells to grow erect, which allows a greater packing of individuals on the substrate leading to higher cell densities. On the other hand, faster current velocity forces cells to grow prostrate, reducing the potential attachment area of substrate for other cells and leading to decreased density. This report presents further investigations of this hypothesis and discusses the physical aspects of community structure.

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MATERIALS AND METHODS

SAMPLING METHODOLOGY AND PREPARATION. This study was conducted on the Maumee River approximately 20 m upstream from the filtration plant near Waterville, Lucas County, Ohio. The Maumee River, which originates in north-east Indiana, flows through the northwest corner of Ohio and empties into the western basin of Lake Erie at Toledo.

Dolomite was collected along the shore of the river near the study site and used as a natural substrate for periphyton colonization experiments. Dolomite is common in the bedrock of northwest Ohio and is exposed along much of the streambed in the Maumee River. The rocks were chosen specifically for their flat, relatively smooth, wafer-like characteristics. They were scoured clean with a toothbrush, broken into pieces with surface areas of about 2.0 cm², and attached to glass specimen stubs with an inert epoxy resin glue. After the glass stubs with attached rocks were secured to plexiglass plates with silicon aquarium sealer, the plates were bolted to concrete blocks. Substrates were placed in the river on 10 February 1980 along a transect across the streambed at a depth of 0.5 m. Current velocity at each block was measured at the top upstream edge of the block with a propeller-driven current velocity meter (Model 2035-MK III, General Oceanics, Inc.). Measurements were taken at the beginning and end of the incubation period. Chemical properties of the river were assumed to be constant owing to turbulent flow at the study site.

After 24 days, the substrates were retrieved from the river and fixed in the field with 4% glutaraldehyde. The substrates were then put on ice and transported back to the laboratory, where they were dehydrated in an ethanol series and critical point-dried with liquid CO₂. Care was taken not to let the samples break the air-water inter-face to ensure the integrity of the natural structure of the community. The air-liquid interface was broken only when the samples were transferred from 100% ethanol to the critical point drying chamber. The samples were then removed from the glass specimen stubs, mounted on aluminum stubs, and sputter coated with gold-palladium. Subsequent observations were performed with a Hitachi HHS-2R scanning electron microscope (SEM) at 20 kV and 25° tilt.

Four of the substrates set out were usable for analysis. Two of the substrates were colonized in a current velocity of 15 cm/s and the other two in a current velocity of 40 cm/s. The surface area of rock analyzed on each substrate equaled 3.075 mm². This was divided into 25 plots (each 1.23 × 10⁻¹ mm²) and photographed. Plot one was assigned to the center of each substrate. Four rows of six plots extended from the center plot at right angles. All micrographs were taken at a magnification of 250X.

All of the diatom data presented were derived directly from the SEM micrographs with the aid of a dissection microscope. Naturally occurring epilithic samples were collected at the same time that the introduced samples were harvested. The diatom component of these samples was cleaned and mounted permanently on glass microscope slides. These were referred to when questions concerning diatom identifications arose during SEM analyses.

ATTACHMENT PATTERNS CLASSIFICATION. The micrographs were analyzed to determine species composition, abundances, and attachment patterns on the substrates. The attachment patterns classification was constructed based on the substrate types and attachment mechanisms. There were three available substrate types recognized for colonization in this study: the rock surface, other diatoms, and mucilage.

The attachment mechanisms were separated into three varieties. First was a prostrate attachment where the cell, from the use of mucilaginous secretions along the length of the diatom valve (Patrick and Reimer 1966), adheres by lying flat on the substrate. Second was an erect-adnate attachment whereby the cell secretes a small mucilage pad at one end of the valve to attach to the substrate allowing it to stand upright (Patrick and Reimer 1966). Third was an erect-stalked attachment where the cell secretes a slender mucilage stalk of variable length from one end (Patrick and Reimer 1966), and where attachment to the substrate projects it away from the surface.

These two components of the attachment patterns generate a classification based on nine categories: prostrate on rock (PR); prostrate on diatoms (PD); prostrate on mucilage (PM); adnate on rock (AR); adnate on diatoms (AD); adnate on mucilage (AM); stalked on rock (SR); stalked on diatoms (SD); and stalked on mucilage (SM) (Fig. 1A-C). Each diatom encountered was identified to species and placed in one of the nine categories.

DATA ANALYSIS. Values of community diversity were generated for each community with Shannon's information measure (H')

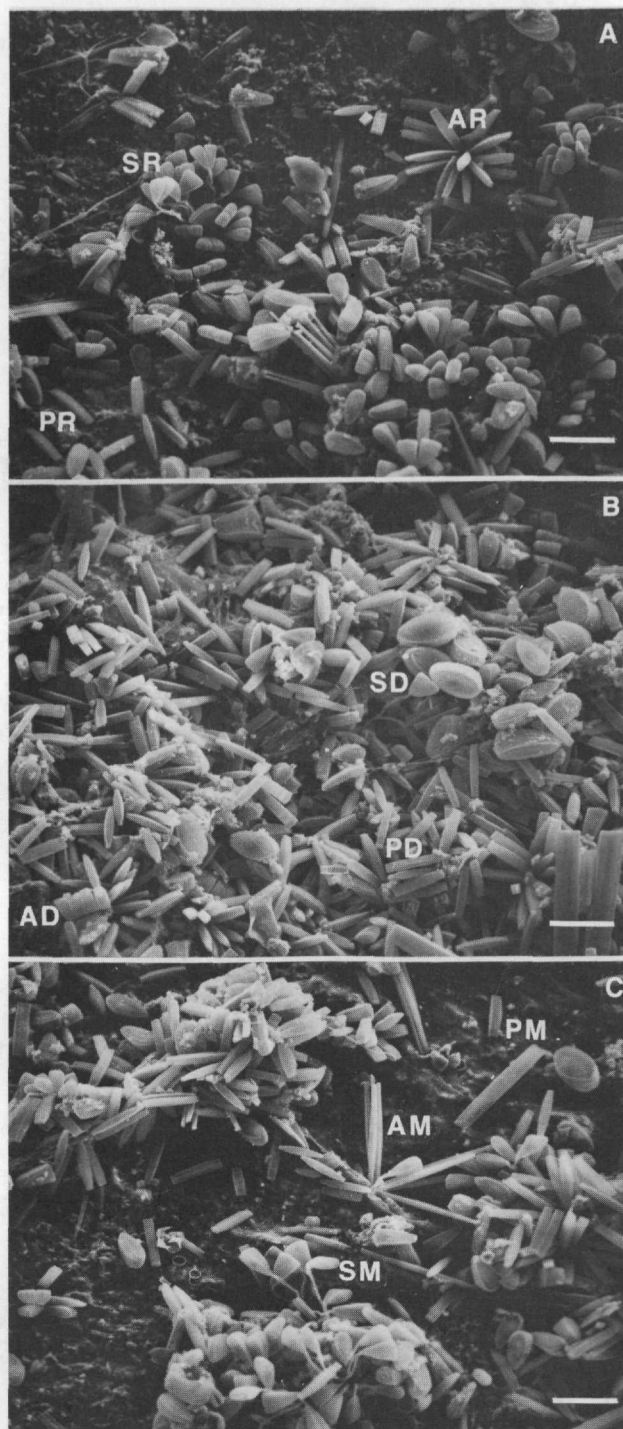


FIGURE 1. Examples of the nine categories of the attachment patterns classification. A. Prostrate on rock (PR), adnate-erect on rock (AR), and stalked-erect on rock (SR). B. Prostrate on diatoms (PD), adnate-erect on diatoms (AD), and stalked-erect on diatoms (SD). C. Prostrate on mucilage (PM), adnate-erect on mucilage (AM), and stalked-erect on mucilage (SM). Bars equal 40 μm.

modified by Hill (1973). Species diversity is estimated by:

$$D = \exp \left(- \sum_{i=1}^s (n_i/N) \ln(n_i/N) \right),$$

where *s* is the number of taxa in the sample, *n_i* is the total number of individuals in the *i*-th taxon, and *N* is the total number of individuals in the community. By using *D*, *H'* is converted to a value describing the equivalent number of equally common species for the community.

Community similarity was calculated with Stander's Similarity Index (SIMI) (Johnson and Millie 1982). The SIMI is determined by:

$$\text{SIMI} (1, 2) = \frac{\sum_{i=1}^T (N_{1i}N_{2i})}{\left(\sum_{i=1}^T N_{1i}^2 \sum_{i=1}^T N_{2i}^2 \right)^{1/2}},$$

where N_{1i} and N_{2i} are the proportion of individuals represented by the i -th taxon in assemblages 1 and 2, respectively, and T is the total number of taxa. Values range from 0 to 1, with 1 indicating the greatest similarity.

Values for niche breadth were calculated for each taxon in both communities by the niche breadth equation in McIntire and Overton (1971). Niche breadth is measured by:

$$B_i = \exp \left(- \sum_{r=1}^Q (n_{ir}/N_i) \ln(n_{ir}/N_i) \right),$$

where n_{ir} is the number of individuals in the i -th taxon found at the r -th habitat, and N_i is the total number of individuals in the i -th taxon found at all Q habitats. Values for B_i are a measure of the equivalent number of habitats in which a taxon is equally common. Values for B_i range from 1 to 9.

RESULTS

SPECIES COMPOSITION. A total of 23,629 cells were enumerated from four samples, two of which developed in a fast current velocity (40 cm/s) and two of which developed in a slow current velocity (15 cm/s). Representative micrographs of the fast- and slow-current communities are presented in Figure 2(A-F).

There were 30 different species identified from all of the samples; 28 of these were species of pennate diatoms. Centric diatoms were combined into one category, as were filamentous algae. The fast-current community had 17 taxa present (three of which were exclusive), with a total of 5,326 cells counted. Its species diversity value was 2.92. The slow-current community had 27 taxa present (13 of which were exclusive), with a total of 18,303 cells counted. The species diversity value was 3.84. Species-area curves were generated on each

replicate to ensure that an adequate sample size was analyzed.

The cell densities per mm^2 of the top 13 taxa whose percent relative abundances were 0.1% or greater are given in Table 1. Total cell densities were more than three times greater in the slow-current community, with nearly all species maintaining denser populations. The effect of current on cell densities was significantly ($P = 0.001$) different using a t -test. The two communities were very similar in species composition, with the noted exception of *Surirella ovalis* var. *brightwellii* whose populations showed a marked increase in the slow-current community. The strong similarity between both communities was borne out by a very high SIMI value of 0.96.

ATTACHMENT PATTERNS CLASSIFICATION. The total relative abundance of each category is given in Table 2, along with the relative abundances of the top three dominants. From the total relative abundances it can be seen that categories PR and AR showed a favorable response to fast current. Categories PM, AM, SM, and SD were used exclusively in the slow-current community. A contingency χ^2 -test was performed to determine if the cell numbers of the two communities were similarly distributed across the nine categories. They were found to be significantly ($P = 0.005$) different. It is apparent that the slow-current community is more evenly distributed across the categories.

Fragilaria vaucheriae heavily influenced the total values in the categories (prostrate and erect-adnate) where it was found. *Gomphonema olivaceum* was the only taxon that was represented in all nine categories. It strongly influenced the AR total values, and was the only taxon using the erect-stalked category. *Surirella ovalis* var. *brightwellii* showed a more minor influence in the PR and PD categories.

TABLE 1

Cell densities per mm^2 , relative abundances (in parentheses), and niche-breadth values for the major taxa in the fast- and slow-current communities. Values given were derived by combining the replicates for each current velocity.

Taxa	Cell density (No./ mm^2)		Niche Breadth	
	Fast	Slow	Fast	Slow
<i>Fragilaria vaucheriae</i> (Kütz.) Peters.	1138.21 (65.7)	3482.93 (58.5)	3.00	4.95
<i>Gomphonema olivaceum</i> (Lyngb.) Kütz.	389.59 (22.5)	812.36 (13.6)	1.37	4.11
<i>Gomphonema parvulum</i> Kütz.	—	8.13 (0.2)	—	3.19
<i>Meridion circulare</i> (Grev.) Ag.	43.25 (2.5)	123.58 (2.1)	1.81	3.07
<i>Navicula cryptocephala</i> var. <i>veneta</i> (Kütz.) Rabh.	17.89 (1.0)	34.47 (0.6)	1.70	2.93
<i>Nitzschia dissipata</i> (Kütz.) Grun.	17.89 (1.0)	63.41 (1.1)	2.10	3.32
<i>Surirella ovalis</i> var. <i>brightwellii</i> Wm. Sm.	36.42 (2.1)	1027.97 (17.3)	1.74	2.58
<i>Surirella ovata</i> Kütz.	4.55 (0.3)	114.15 (1.9)	1.51	2.50
<i>Synedra acus</i> Kütz.	0.33 (0.02)	52.68 (0.9)	1.00	3.48
<i>Synedra ulna</i> (Nitz.) Ehr.	—	20.16 (0.3)	—	2.98
<i>Synedra</i> sp. 1	0.98 (0.06)	26.67 (0.04)	1.89	2.80
Centric spp.	72.52 (4.2)	167.15 (2.8)	1.76	2.94
Filamentous algal spp.	7.15 (0.4)	2.93 (0.05)	1.82	3.37
TOTAL	1732.03	5952.20		

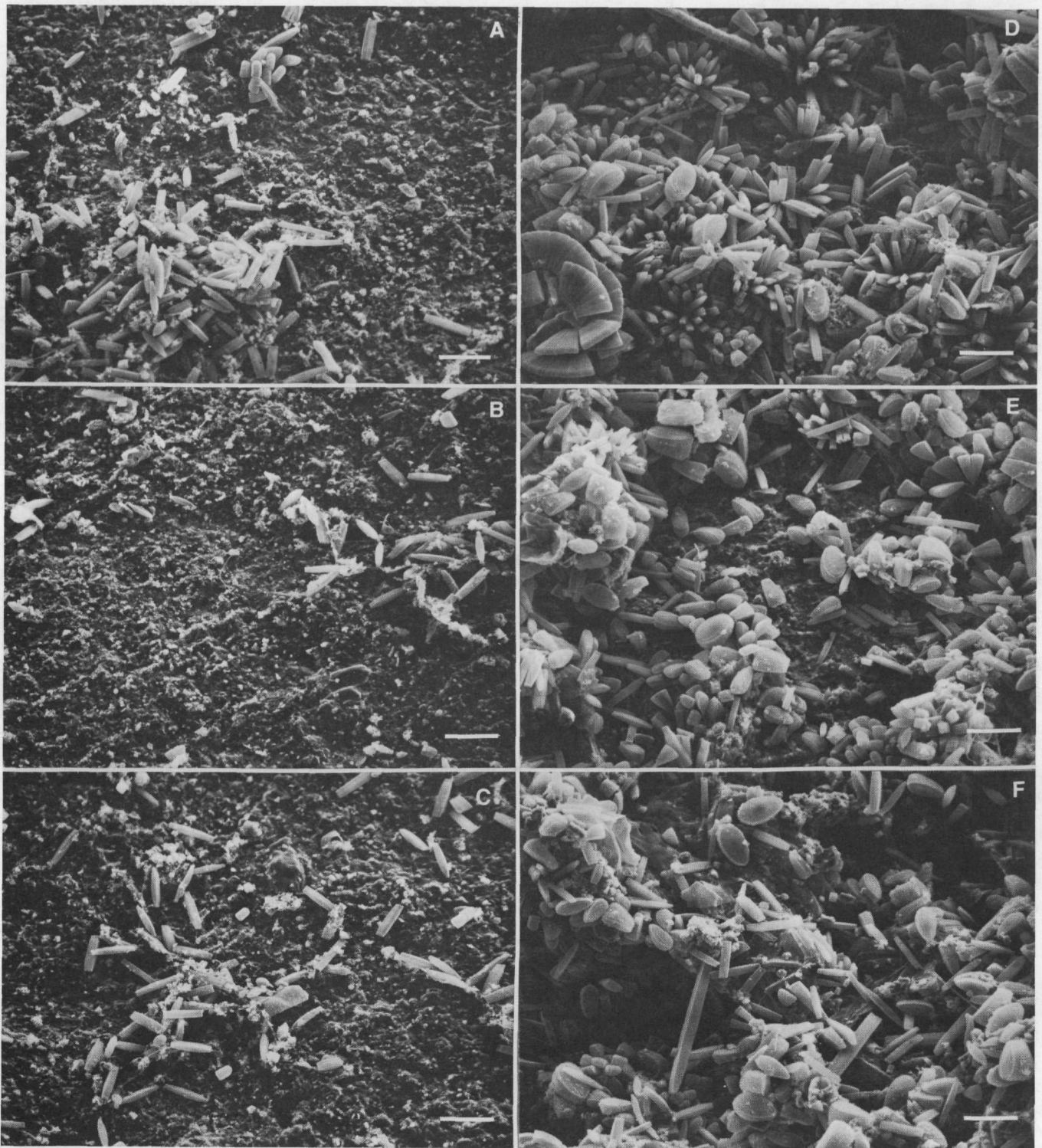


FIGURE 2. Representative micrographs of the fast (A-C) and slow (D-F)-current communities. Note the varying degree of densities demonstrated within and between each current speed. A mat of mucilage can be seen in micrograph F. Bars equal 40 μm .

Niche breadth values were calculated from the attachment patterns classification, where Q categories equal nine (Table 1). In all taxa, the niche breadth values and B_{total} were largest in the slow-current community.

DISCUSSION

The diatom community in the slow current was very similar in species composition to the community in the faster current. The most pronounced difference between

the two was the greater cell densities in the slow current. However, the findings here do not clearly support our original hypothesis (Lamb and Lowe 1981). Low cell densities in the fast current were not related to a high percentage of prostrate cells and a low percentage of erect cells. The largest percentage of cells were using a prostrate means of attachment (spread out over PR and PD) in the fast current as expected; however a considerable number of cells were also using an erect-adnate attach-

TABLE 2

Relative abundances of total cells and *Fragilaria vaucheriae*, *Gomphonema olivaceum*, and *Surirella ovalis* var. *brightwellii* for each position of the attachment patterns classification in the fast- and slow-current communities.

Category*	Current velocity	Total	<i>Fragilaria vaucheriae</i>	<i>Gomphonema olivaceum</i>	<i>Surirella ovalis</i> var. <i>brightwellii</i>
PR	Fast	36.7	28.4	1.3	1.6
	Slow	24.7	12.8	0.34	8.3
PD	Fast	20.1	17.9	0.24	0.51
	Slow	30.1	18.7	0.15	7.3
PM	Fast	—	—	—	—
	Slow	8.5	5.5	0.07	1.7
AR	Fast	42.8	19.2	20.8	—
	Slow	23.6	14.5	7.2	—
AD	Fast	0.36	0.28	0.08	—
	Slow	5.1	4.3	0.73	—
AM	Fast	—	—	—	—
	Slow	3.9	2.7	1.0	—
SR	Fast	0.04	—	0.04	—
	Slow	3.3	—	3.3	—
SD	Fast	—	—	—	—
	Slow	0.26	—	0.26	—
SM	Fast	—	—	—	—
	Slow	0.62	—	0.62	—

*Key: PR = prostrate on rock; PD = prostrate on diatoms; PM = prostrate on mucilage; AR = adnate on rock; AD = adnate on diatoms; AM = adnate on mucilage; SR = stalked on rock; SD = stalked on diatoms; SM = stalked on mucilage.

ment. Additionally, higher cell densities in the slow current did not reflect a high percentage of erect cells. The largest percentage of cells were still using a prostrate means of attachment.

In general, total cell densities decreased from prostrate to erect-adnate to erect-stalked for all substrates in both communities. Total cell densities decreased also from rock to diatoms to mucilage for all attachment mechanisms in both communities. It appeared that regardless of current velocity, development was similar in each community. Larger niche-breadth values in the slow current reflected the wider use of attachment mechanisms and substrate types. The forces generated by the swifter current appeared to retard community development.

Of considerable importance to periphyton communities and observed from the attachment patterns classification was the invasion of the vertical dimension by diatom populations. Many investigators have reported on the invasion of the third dimension (height) as part of an often predictable pattern of diatom colonization and subsequent community succession (Patrick 1976, Marszalek et al. 1979, Patrick and Roberts 1979, Hudon and Bourget 1981, Hoagland et al. 1982, Korte and Blinn 1983). Classically, there is an initial stage of substrate conditioning where bacteria, fungi, and organic matter attach first. Then low-profile diatoms become established. These include prostrate forms and erect-adnate forms of short stature. These are followed by the taller erect-adnate forms and the stalked diatoms. Filamentous algae can then invade the height dimension even further.

The advantages of vertical development appear to be two-fold. First, the competition for substrate surface area is reduced (Hudon and Bourget 1981, Hoagland et al. 1982). The second advantage is that the diatom positions itself further up in the flowing water. In this position,

the cell receives more light, nutrients, minerals, and greater gas exchange (Whitford 1960). The metabolism of the cell is increased and it grows faster.

With cell densities decreasing from prostrate to erect-adnate to erect-stalked, the data presented here indicate the existence of community succession by gradual vertical invasion. In the early stages of development, succession occurs more quickly in slow-current communities, as shown by the greater use of the erect and stalked attachments and by the greater niche-breadth values. Evidently, the fast current at least initially retards the development of periphyton communities, supporting the observations of previous investigators (McIntire 1966, Steinman and McIntire 1986).

Also of importance and observed from the attachment patterns classification was the generation, use, and succession of substrates within the community. A larger percentage of cells used more substrate types in the slow current. Almost 80% of the cells adhered to the rock surface in the fast-current community. On the other hand, only 51% of all cells were found on the rock surface in the slow current. Diatoms and mucilage were being used as the substrate types. The generation of more usable substrates by the community was probably essential to its development.

Previously-colonized diatoms seem to have an important role as new substrates. To attach to a substrate in a river, a diatom must pass through a decreasing gradient of laminar currents that become established next to the surface of a substrate (Hynes 1970). Once it becomes established, it slightly disrupts the laminar flow in its wake producing a minute zone of microturbulence. Others have shown that colonization is enhanced in zones of microturbulence (Munteanu and Maly 1981, Stevenson 1981). One attachment enhances the possi-

bility of future attachments by altering the substrate surface conditions. Therefore, during the early stages of immigration, diatoms use each other as new substrates. The attachment patterns classification used in the present study seemed to indicate that diatoms are the next primary substrate for new colonizers. Stronger forces in the faster current retarded initial colonization, thereby checking the use of diatoms as a substrate by diatoms.

As immigration continues, more mucilage accumulates and becomes an important component within the community. Perhaps more important than the use of mucilage as an attachment mechanism is its continual secretion after attachment has been established. Massive accumulation of mucilage has been noted by others who have described its importance to the community. The adhesive properties of mucilage make it a sticky substrate for enhancing immigration and diversity (Stevenson 1981, Hoagland et al. 1982); binding organic matter into the community, thereby making it nutritionally richer (Paul et al. 1977, Hoagland et al. 1982); stabilizing and supporting the physical structure of the community (Allanson 1973); and securing individual cells and layers of cells into the community, protecting them from the current (Blum 1962).

In the present study, the accumulation of mucilage within the community represented the third substrate type. It probably followed diatoms as the next major substrate for colonization. The use of mucilage as a substrate was restricted entirely to the slow-current community, and was reflected in the larger niche-breadth values. It is likely that faster current velocities hinder the accumulation of mucilage because immigration is initially inhibited.

In summary, comparison of the fast- and slow-current communities in this study allowed us to draw conclusions about the direction of community development (i.e., development is similar in both, with maturation being quicker in the slow current). We found a gradual vertical development by comparing the two communities from the attachment patterns classification. There appeared to be a gradual succession from rock to diatoms to mucilage as the primary substrate type. We also found that vertical development and the use of successive substrates occurred concurrently.

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